GULF BIOLOGIC STATION

CAMERON, LA.

BULLETIN No. 13

SOME OBSERVATIONS

ON THE

Motile Leaves of Erythrina Herbacea

BY

F. H. BILLINGS, Ph. D.

ISSUED BY THE

Louisiana State Board of Agriculture and Immigration

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*Died Jan. 16, 1909.

SOME OBSERVATIONS

ON

The Motile Leaves of Erythrina Herbacea.

During a part of June, 1908, the writer was in residence at the Gulf Biologic Station. At this time some observations were made on the motile leaves of Erythrina herbacea, an herbaceous, almost shrubby, plant locally occupying more or less shady places on a low ridge near the Station building. The ridge was partially covered with a growth of stunted trees, principally Xanthoxylum clava herculis, Crataegus, Bumelia lanuginosa and Celtis mississippiensis. The thickets formed by these trees were sometimes quite dark, though the more usual occurrence was a more open growth with interspersed clumps of stunted trees. The favorite habitat of Erythrina herbacea appeared to be the edge of such clumps, where they received a one-sided illumination. Many plants, however, were found in extremely shaded places into which direct sunlight never penetrated. It was not common to find them in exposed situations.

Erythrina is mostly a tropical and subtropical genus, the species under discussion being distributed, so far as this country is concerned, through our southern states.

The leaves of Erythrina are three-foliate, each leaflet bearing a pronounced pulvinus, or motile organ, in common with many Leguminosae.

Motility of leaflets is a phenomenon well distributed through the Leguminosae and Oxalidaceae, the species varying among themselves in the degree of sensitiveness to light and the rapidity with which they respond to paratonic stimuli. Erythrina is not to be considered in the class with mimosas, sensitive to mechanical shock, but rather with those plants whose leaves respond merely to varying degrees of light intensity. The classic representative of such is the common garden bean (Phaseolus). This plant has long been known to possess the power of adjusting its leaflets into three definite positions corresponding to the intensity of illumination. One is the so-called sleep position which is assumed in darkness, and in which the leaflets turn so as to point vertically downwards. In this position the spongy paren-

chyma of the two lateral leaflets face each other. A second is a diurnal one in which diffused light or moderate sunlight is brought to bear upon the leaves. The leaflets assume an expanded position so as to bring their palisade surfaces against the light and approximately at right angles to it. The leaflets would lie nearly in the same plane. A third position is that assumed in the intense sunlight of midday. The leaflets turn vertically or edgsewise, so as to bring their surfaces at an acute angle with the light rays, if not parallel with them.

The purpose of the "sleep" position is generally stated to be the checking of radiation of heat whereby plants would be enabled to withstand a lower temperature. Darwin has shown that this actually works in practice; but such a theory is worthless when plants of tropical lowlands are considered, since danger of injuriously low temperatures never exists.. Stahl suggests a possible purpose in the more efficient shedding of dew, so that transpiration could proceed with less interference.

The manifest purpose of the extended position of the leaflets is to bring them into favorable light relation.

The edgewise position prevents a dangerous exposure to too intense sunlight, for it has been shown that chlorophyll is injured by such exposure. Credit is sometimes given to the belief that lessening of transpiration is accomplished by huddling of the leaves, since by overlapping, their exposed surface is reduced. Transpiration would be diminished by the decrease in temperature resulting from reduced illumination, or by bringing stomata-bearing surfaces into contact with other leaf surfaces. In Erythrina, the under or stomata-bearing sides of the leaflets are not brought together, but face outwards, resulting in greater exposure probably than when they lie parallel to the ground. In some instances there is no attempt made to overlap the leaflets, as sometimes occurs in Phaseolus. Instead of bending its leaflets up or down, a horizontal leaf will rotate them ninety degrees, leaving them still extended with their midribs in a horizontal position.

Erythrina herbacea will probably be found not to differ from many tropical plants, as soon as their leaves are investigated. It differs from Phaseolus in the time required for a response to variation in light intensity and in the behavior of its leaflets in direct sunlight. Part of the experimentation on rapidity of response to changes in light intensity was made on a plant of low stature, growing in a dark thicket to which practically

no direct sunlight was admitted. Trees were cut down in the immediate neighborhood of the plant, so that the sun would shine upon it between 11 in the morning and 4 in the afternoon. The plant had young leaves which had not reached their full size and which were further distinguished by their light green color. It also had mature leaves of a dark green color. It was found that the younger leaves were, on the whole, more quickly responsive than the older ones.

The plant was small enough to be easily covered with a soap box. When covered in the evening, the plant showed a "sleep" position when the box was removed at any time during the day. This position in Erythrina is not as pronounced as in Phaseolus, Desmodium or Oxalis. The leaflets have a downward trend, but do not approach so nearly the vertical position.

FIGURE 1.—Erythrina herbacea with leaves in the so-called "sleep" position.

Under natural conditions, the leaves are hardly ever exposed to direct sunlight while still in the sleep position. The diffuse light of the day, preceding sunrise, would be sufficient to induce the expanded condition.

The first experiment upon the plant in question was to determine the time required for a leaf to pass from the sleep position into the position taken in intense sunlight. The lateral leaflets were selected for experiment rather than the terminal one as the extreme intense sunlight position was much more easily determined. It was not an easy matter to tell just when the terminal leaflet had finished its upward bend, but in the laterals no further motion was possible as soon as the surfaces came in contact. The experiment was set up by covering the plant with a box the night before and then uncovering it suddenly during the period of greatest sun intensity. The leaflets being in the sleep position, had considerably over ninety degrees to travel in order to reach the vertical position. From ten to fifteen minutes elapsed before any response was noticeable, but when the leaflets had reached the horizontal position, their motion was rapid, since they reached the extreme vertical position by the end of thirty minutes. The greater part of the motion, therefore, was accomplished during the latter half of the time. If leaves in the expanded condition were used at the beginning of the experiment, the time required for lateral leaflets of young leaves to attain extreme edgewise position was found to be nine minutes. An older leaf required twelve minutes. In large plants with large leaves, long since mature, the time required may be as much as twenty to thirty minutes. It generally happens in such plants that the lateral leaflets do not come into actual contact, though they may reach a very acute angle.

FIGURE 2.—Erythrina plant in shade, showing expanded condition of leaves.

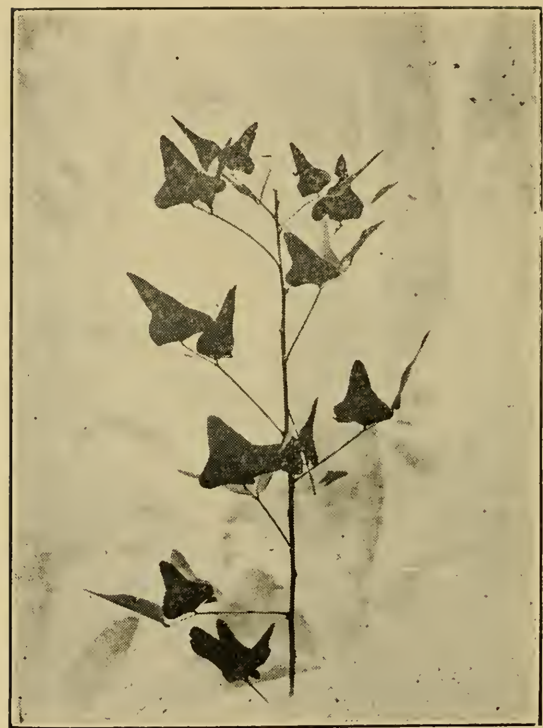

FIGURE 3.—Same plant as in previous figure after exposure twenty-five minutes to full sunlight.

The sensitiveness of the leaflets to direct sunlight is considerable as can be seen from an examination of plants having an eastern exposure. Soon after the sun began to shine upon them

FIGURE 4.—Same plant as in two previous figures after prolonged exposure to full sunlight.

early in the morning, their leaflets began to turn towards the east, so that before 8 o'clock (in June) the edgewise position was reached. At this time of day the sun's heat is not at all intense, so that one is led to believe that it is light rather than heat that acts as the stimulus to motion. Further proof of sensitiveness to light is seen in the response to strong diffuse light such as prevails at midday. Leaves which are not too greatly shaded turn their leaflets partially towards the light, though, of course, not to the extent that they do in full sunlight. If a plant is covered by an umbrella early in the morning, and is examined at midday while still covered, its leaves show an upward turn which is evident though not pronounced. Leaves

equally shaded in a dark thicket and never exposed to direct sunlight, show no upward turn. In the first instance, the plant had been accustomed to daily exposure to sunlight at midday, and hence the motion in its leaves is probably due to the after effect. No such after effect would be possible, of course, in a plant continually shaded.

While the position of the leaflets in direct sunlight is an edgewise one, and while such a position in the case of the lateral leaflets might be reached by a mere twist of ninety degrees, Erythrina prefers to bend the pulvini in attaining it. In all cases there is an attempt on the part of the plant to bring the tip of each leaflet toward the sun rather than the side edge. For instance, if a leaf lies horizontally, its leaflets expanded, with their spongy parenchyma sides downwards, the pulvini by twisting would bring their blades edgewise. Ethyrina, however, bends its pulvini ninety degrees upwards, thus bringing the tips of the leaflets towards the sun. If a leaf lies with its midrib pointing directly upwards, its terminal leaflet towards the sun, the expanded position of the leaf would mean an edgewise position for all its leaflets. Thus they would all be protected from intense sunlight. Yet the tips of the lateral leaflets point outwards, not upwards, and so a bend in their pulvini occurs which results in their tips being directed towards the sun. Such position has in it no greater merit as a protective feature than the expanded one, unless it be the huddling of the leaflets and a consequent slight reduction of transpiration in the terminal leaflet.

In the extreme direct sunlight position of the leaflets in Erythrina, the under or stomata-bearing surface is outwards or exposed to diffuse light and to wind. As was mentioned near the beginning of the paper, such an arrangement is scarcely conducive to lessening transpiration. If this is the desideratum, then a method having a semblance of efficiency, would be a vertical position with tips downwards so that the stomata-bearing surfaces might be together. As this does not occur in Ethyrina, it is reasonable to suppose that so far as this species is concerned, too great light intensity is feared rather than too rapid transpiration.

An *a priori* conclusion as to the rapidity of assumption of the expanded condition following closure due to direct sunlight, is

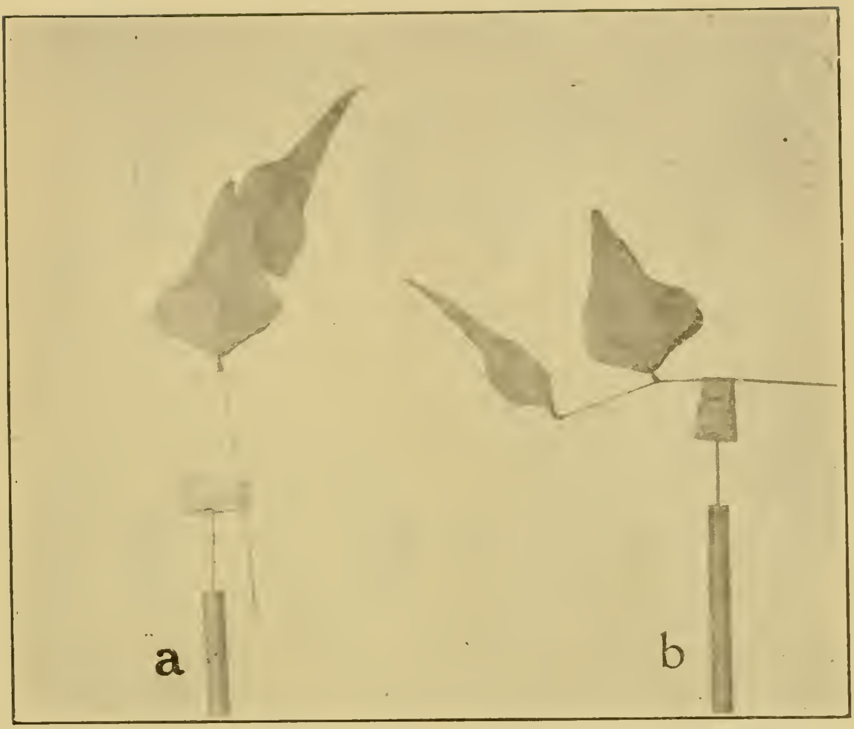

FIGURE 5.—Leaflets of Erythrina showing position in extreme sunlight; a, when leaf midrib is vertical; b, when it is horizontal. Taken about 11:30 A. M.

that more time would be consumed. Reasons for such a belief are at least two. One is the absence of such a powerful stimulus as direct sunlight. A second is the lack of urgent need for quickly altering the position, since diffuse daylight or darkness are in no way dangerous to the chlorophyll. The cause for the return to the expanded condition may be either the absence of the exciting influence of direct sunlight, or, in case of exposure to diffuse daylight, to the desire on the part of the leaflets to be at right angles to the light rays; or, if exposed to darkness, to a desire to assume the sleep position. If the first alternative were true, it would presuppose a neutral position into which the leaflets would fall as soon as the exciting stimulus were removed. Just what this neutral position is, is uncertain. There is considerable doubt as to whether such a position exists. The so-called

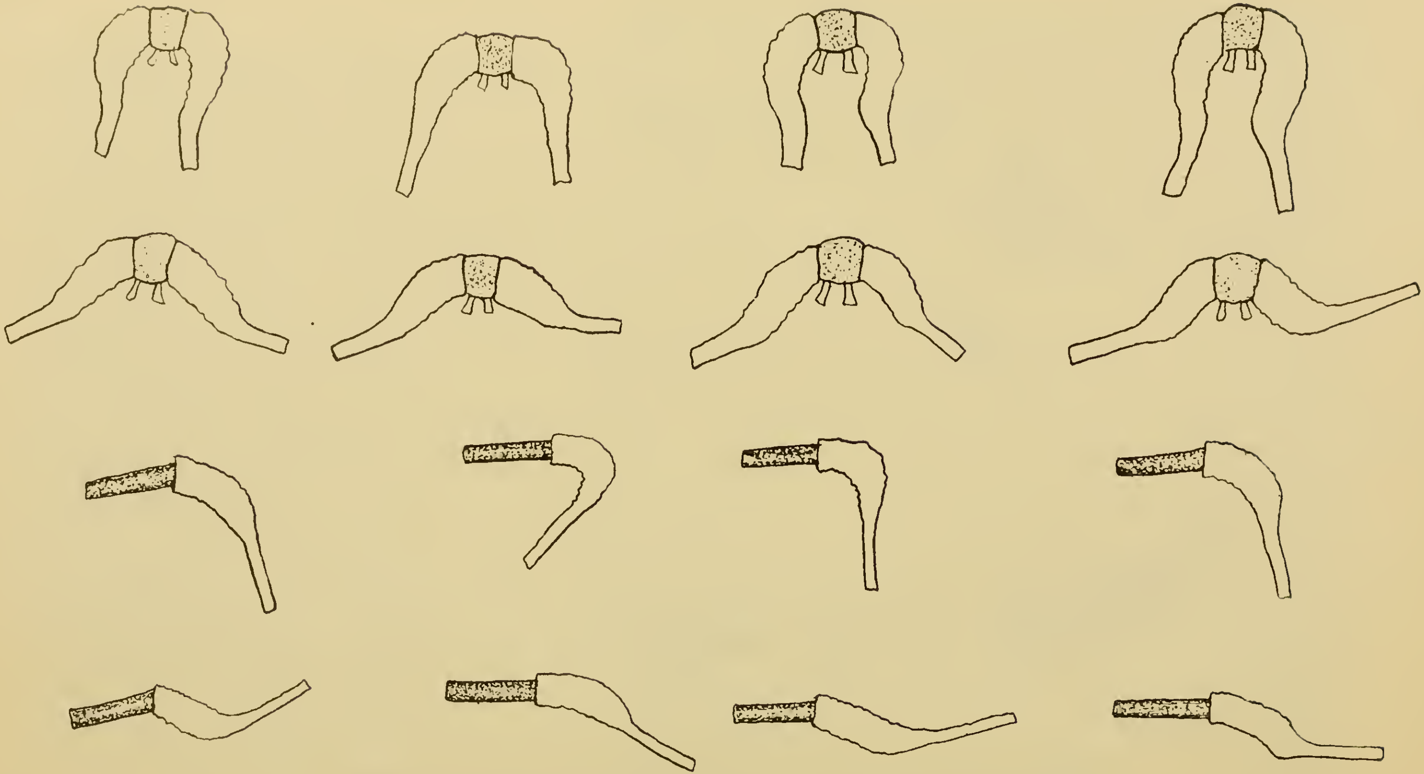

Figure 6.—Diagrams of pulvini in shade and sunlight. First row across terminal pulvini from four leaves in shade. Second row, same pulvini after exposure to sunlight. Third row, pulvini from four pairs of lateral leaflets in shade. Fourth row, same pulvini after exposure to sunlight. Shaded part in each case is midrib in leaf.

sleep condition might answer, could it only be proven that no stimulus is responsible for it, or that no advantage is gained by assuming such a position.

It is generally believed that sleep movements are adjustments to environment, either to diminish radiation or to facilitate shedding of water, such as dew. There is, therefore, no reason for believing that a neutral position exists. On the contrary, the leaves are probably continually in adjustment to external conditions or stimuli.

Experiment showed that the facts warranted the conjecture that greater consumption of time was found to be necessary for the leaflets of Ethyrina to return to the expanded condition. The previously-mentioned plant of low stature was used for the test, but so much variation existed among the different leaves that very definite results were not possible. Some leaves responded fairly quickly, so that in twenty minutes they were nearly expanded. At the end of this time, however, others were half expanded, while yet others were turned upward, having shown little or no inclination to change position.

If leaves were artificially placed in unusual relation to sunlight, the tips of the leaflets continued to point toward the light. A leaf with its back or spongy parenchyma up, turned its leaflets vertically toward the sun, thus bringing the spongy sides of the lateral leaflets together. If a leaf is turned edgewise to direct sunlight, with the midrib perpendicular to the rays, a movement of the terminal leaflet occurs, although it is already in a protective position. It deflects its tip upwards, its surface being maintained in the same plane. A bend in its pulvinus of less than ninety degrees is the rule. The lateral leaflets remain stationary. Both are protected, and one has its tip directly toward the light. The lower leaflet has its tip pointed downwards. It would be a difficult matter for this leaflet to turn its tip toward the light, for it would have to swing into the horizontal position first, or else rotate its pulvinus one hundred and eighty degrees. The first alternative would bring its surface perpendicular to the sun's rays, which, of course, it is trying to avoid. The second is not within the power of the pulvinus. Another factor, probably of greater importance, and doubtless the real reason for the leaflet's stationary position,

is the fact that the pulvinus is approximately equally illuminated on all sides.

The deflection of the terminal leaflet upwards is explainable on the ground that the pulvinus is illuminated on one side greater than on the opposite.

In diffuse one-sided light, the leaflets endeavor in general to assume that relation with the light that their palisade surfaces would lie perpendicular to the rays and toward their origin. When the midrib is horizontal and the light is from above, the expanded position results. It is of some interest to notice the behavior of the leaflets when placed at various angles with the direction of the diffuse ligth. An experiment was arranged in which small vials, filled with water, were inserted in holes in a horizontal wooden cylinder. The holes were bored in such a way that the bottles would stand out at different angles. A leaf in the expanded condition was placed between the grooved split halves of a cork in each vial. Care was taken to remove the leaves under water and use them at once, although experience had already shown that they remain turgid and sensitive to light for several hours after abscision. If kept turgid by being placed in water or in a moist chamber, their sensitiveness will continue for over a day. Hence on account of their quickness to respond to light, there was practically no danger of abnormal results. Leaves were placed by an open window in the following four relations to the light:

90° to light, edgewise.

90° to light, spongy side upward.

Tip of terminal leaflet toward light.

Horizontal (150° to light) pointing from light, with palisade side up.

In the first instance, 90° to light and edgewise, a 90° twist on the part of the pulvinus of the terminal leaflet would bring the blade into a proper light relation. With the lateral leaflets, a 90° deflection of each leaflet in the same direction would produce the desired result. The results of the experiment did not, however, fully coincide with those which one might think ought to occur. The terminal did seemingly attempt to approach the perpendicular-to-light relation, but a twist of about 45° only was attained. The lower lateral leaflet responded slowly, rising after a time to an oblique angle with the light. Only the

upper lateral leaflet responded at once in assuming a perpendicular-to-light position. The difference in behavior of the two lateral leaflets may be at least partially explained by noting that the lower was partly if not entirely shaded by the upper. There is no doubt but that the terminal leaflet would, if it were on the plant, and if it were given time enough, attain a perpendicular relation; but when compared with the hinge-like bending of the laterals, a twist is a motion requiring considerable more time.

In the second instance, the terminal leaflet would require a turn or twist of 180° to bring the palisade surface toward the light. The laterals could reach that position only by a movement of equal amplitude.

Only the terminal leaflet succeeded in reaching an approximately perpendicular position, and this was accomplished by an upward and then backward bending. The response of the lateral leaflets was always quick and uniform. They turned into the edgewise position with their spongy tissue surfaces together, and their tips toward the light. Thus they passed into a position

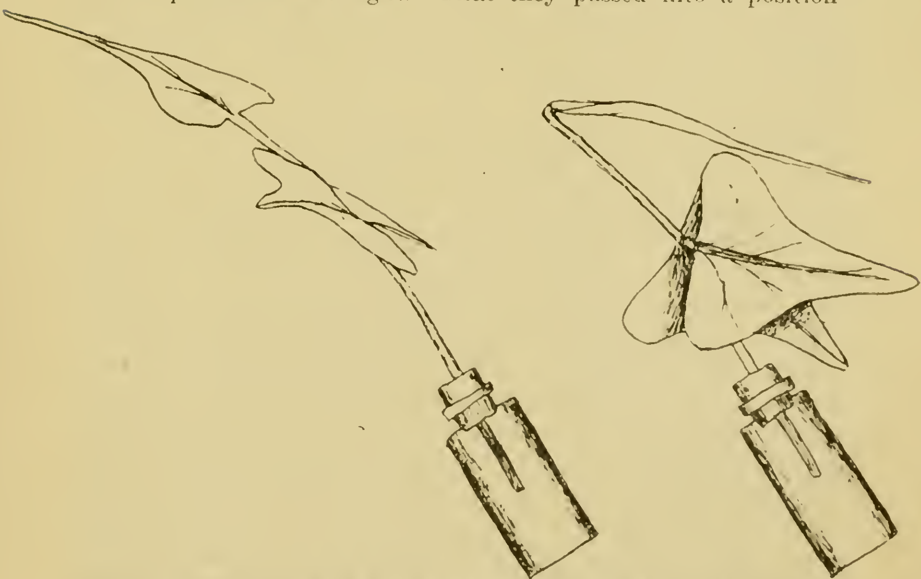

FIGURE 7.—Leaf before and after exposure to diffuse light for 30 minutes. The light rays were from the right and above, and approximately at right angles to the leaf surface. The spongy parenchyma side of the leaflets was toward the light.

similar to that assumed in direct sunlight. It is interesting to note that this light relation was preferred to one with the spongy

parenchyma directly toward the light. In the back-to-back, edgewise arrangement neither side received direct illumination, but nevertheless a normal condition was established in that the palisade side obtained more light than the spongy side. One could conclude from that, that insufficient though proper distribution of light on the two sides of leaflets was more desirable than sufficient light intensity on the wrong side.

In the third instance, a downward turn of 90° of the terminal leaflet would adjust it perpendicularly to the light, and a twist of 90° on the part of the lateral leaflets would place them also in a proper light relation. These movements occurred abundantly in the field as could be seen by examining plants having one-sided illumination. The laboratory experiments repeated them.

In the fourth instance, the expected happened as in the previous experiment. The terminal leaflet turned up to bring the palisade surface toward the light, while the laterals twisted.

The pulvini behaved much like ball and socket joints. The pulvinus of the terminal leaflet can twist 90° in either direction, or 180° in all. Its amplitude as a hinge joint is at least 300°. The pulvini of the lateral leaflets can twist 90° in either direction, or 180° in all, and can bend at least 90° in any direction, giving them an extreme amplitude of 180°.

Twisting and bending may occur simultaneously, thus producing a motion permissible in a ball and socket joint.

The base of the midrib of the leaf is provided with a large pulvinus, but it is neither responsive nor motile to anything like the extent that is the case with the leaflet pulvini. The midrib itself is stiff and straight to the place of attachment of the first pair of leaflets. At this point a difference in direction is usually taken by the remaining portion of the midrib, and in certain instances this difference in direction is undoubtedly accountable by the attempt to bring the terminal leaflet into a more favorable light relation, for instance, out of the shadow of the lateral leaflets, when they happen to lie in the path of the light. Slow changes take place in the midrib pulvinus when the main stem becomes so altered in direction that certain leaves find it difficult to get proper access to the light.

The pulvini of the leaflets are at once the organs for receiving and responding to a light stimulus. The latter point has been

sufficiently dwelt upon. That the pulvini themselves, not the blades, receive the light stimuli in response to which their motion occurs in direct sunlight is demonstrable in several ways. Abscision of the blades does not prevent the pulvini turning upward in direct sunlight; nor does covering the blades with tinfoil or black paper. While such results show that the pulvini are susceptible to light stimuli, others prove that the bades are not likewise susceptible. To demonstrate that pulvini alone are sensitive to direct sunlight whereby they turn their blades edgewise, it was found necessary to preserve the blades intact, and shade the pulvini. A plant was therefore so placed that it would be partly in the shadow and partly in the direct sunlight. One of the leaves in the sunlight was used for experiment, all the other leaves on the plant serving as controls. The leaf in question was in an expanded condition, as were all the others. A narrow piece of cardboard was so placed as to cast a shadow wide enough to just cover the pulvini of the lateral leaflets. The blades were therefore exposed to full sunlight. This leaf, together with those entirely in the shade, showed no sign of turning the leaflets edgewise. Those entirely exposed to sunlight, on the contrary, responded quickly and soon had their leaflets pointed toward the sun.

Hence while the blades are the organs probably directly benefited by such paratonic movements, they depend on their pulvini for sunlight stimulation and for shift of position.

It would appear that a contraction of that part of the motile organ takes place on which the sun shines. This applies to whatever side of the pulvinus is intensely illuminated. The result is a bend in the pulvini of approximately 90°. There is little or no twisting motion induced by intense illumination.

Quite another problem presents itself when the behavior of leaflets under *diffuse daylight* is considered. The pulvini may be unequally illmuinated, but the results of such variation are not consistent unless the blades are taken into consideration. Two leaves, for instance, both in the expanded condition, were placed each in a different light relation. One was turned with its tip toward a source of diffuse or reflected light, the rays lying parallel to the midrib. The other was placed with its midrib perpendicular to the light rays and with the spongy parenchyma turned toward the light. In the first instance the

pulvini of the lateral leaflets would be perpendicular to the direction of light, and except that a relatively different side was illuminated, this was the same light relation of the lateral pulvini in the second instance. Experiments had previously shown that in direct sunlight all sides of the pulvini were sensitive to light and responded in the same way no matter which side happened to be illuminated. If pulvini alone be considered we might have expected similar responses in the two leaves mentioned above. Different results, however, actually occurred. In the first leaf, a twist of 90° occurred in the lateral pulvini, thus bringing the blades perpendicular to the light. In the second leaf, a bend of 90° occurred, accompanied at times by a slight twist.

The terminal leaflets shifted by a bend in both instances, though the illumination was one-sided in the second leaf, and uniform on all sides, practically, in the first leaf.

If, instead of the first leaf mentioned above, one had been taken that was placed edgewise, though perpendicular to the light, it would have been found that the terminal leaflets behaved differently, though the pulvini were similarly placed respecting the light, except, of course, that a relatively different part of each pulvinus was illumined.

In the first leaf a twist occurred, while in the second a bend took place. It would therefore seem from these experiments that the pulvini are not the organs that receive diffuse light stimuli. Contraction on the illuminated side does not occur, nor does there seem to be any relation between the direction of light as regards the pulvini, and their response in motion. When the blades are considered, however, they are found to be the determining factor, since to bring their palisade surface perpendicular to and toward the light, or so that this side will receive more light than the other, is the object of all movements in diffuse daylight. When this has been accomplished, motion due to paratonic stimulus ceases, no matter what the relation of the pulvinus to the light may be.

The response in motion to intense sunlight is more quickly attained than the response to diffuse light. One reason has already been assigned for this, and that is the greater intensity of the stimulus. Another factor should be considered, however, as there is a difference in distance between the light stimulated cells and

those that induce the motion. Just which cells of the pulvinus are the sensory ones is problematical, but, of course, they can not be farther removed from the motion-producing cortex than the epidermus surrounding the cortex. How fast the stimulus travels from the blade to the pulvinus cortex is also problematical, but in any case it has a greater distance to go, and hence would likely require more time than when all is included within the pulvinus itself. This may or may not be the sole cause of the difference in time of response, or it may be one of two or more factors which, acting together, account for the difference.

The final point to be considered is the structure of the pulvinus. While this organ has not been studied in Erythrina, there is no reason to believe that it differs in essential respect from the pulvinus in other Leguminosae. All agree in having an axial strand of vascular tissue, which, as has been shown by Pfeffer. Sachs and others, is in the form of a solid rather than a hollow cylinder. This feature is to permit flexibility. The hollow cylinder arrangement of the bundles with a central pith prevails in the midrib of the leaf where rigidity is desirable, but as they enter the pulvinus, they pass to the axial position

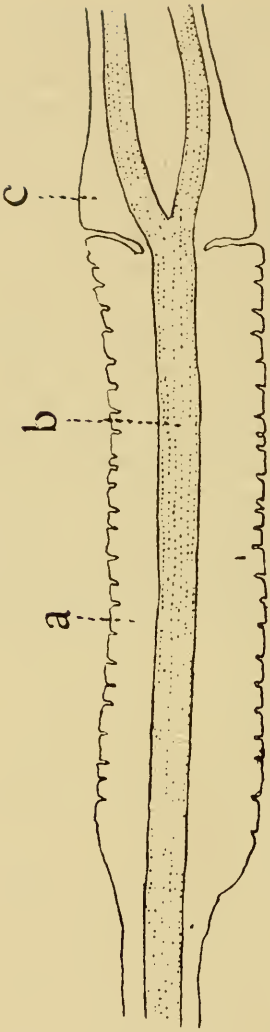

FIGURE 8.—Diagram of a longitudinal section through a pulvinus of a terminal leaflet; a, cortex; b, vascular bundle of pulvinus; c, terminus of midrib of leaf.

with elimination of pith. Surrounding the vascular region is a much-thickened cortex of parenchyma which constitutes par excellence the motile organ. The direct cause of motion has been shown to be a difference in turgescence, or osmotic pressure in the cortical cells on opposite sides of the pulvinus. Osmotic pressure is reduced under the influence of sunlight, for instance, in those cells directly illuminated. That reduced pressure is

accompanied by diminution in the size of the cells, is manifest when a comparison of two sides of a pulvinus is made. In order to show this clearly, pulvini exposed to full sunlight and

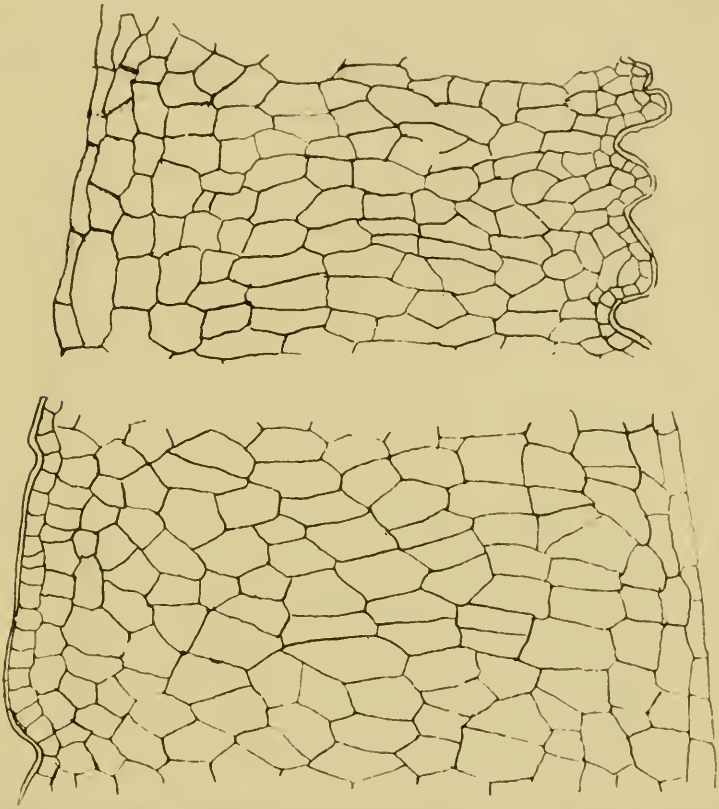

FIGURE 9.—Camera lucida drawings of the cortex on opposite sides of a pulvinus in full sunlight. The upper figure is from the concave or illuminated side; the lower figure is from the under or convex side.

to darkness (sleep position) were used. These were abscised in the field and placed into various killing fluids as Carnoy's fluid, alcoholic solution of corrosive sublimate, and chromo-acetic acid. After embedding in paraffine, sections were made longitudinally.

A comparison in the size of the cells on the upper and lower sides of the pulvini is readily obtained from Figures 9 and 10. The cells on the concave sides in both cases are narrower than

those on the opposite side. The pulvini are cross-grooved, the furrows assisting the bending by permitting compression and expansion the more easily. A very deep groove is located at the point of convergence of the vascular bundles. A deepening of the smaller furrows, together with an increase in their number, occurs on the side that is compressed. A consequent smoothing out process is apparent on the opposite side.

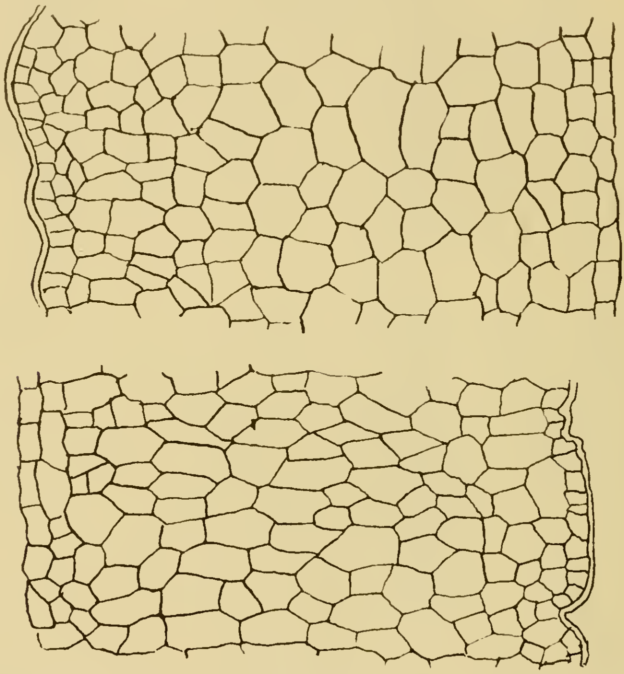

FIGURE 10.—Camera lucida drawings of the cortex on opposite sides of a pulvinus from a leaf in the "sleep" position. The upper figure is from the convex side.